

## The biogeography of scorpions

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**The biogeography of scorpions.** - The biogeographic patterns observed among modern scorpions are the consequence of three major events which can be integrated in the scheme of scales proposed by Udvardy. The distribution of the principal modern groups (i.e. families and genera) is derived from elements (protofamilies and protogenera of Pulmonate-Neoscorpionina) which originated in Laurasia and Gondwanaland during Pangean times. I suggest the following. I. The main factor in the phylogenetic/palaeobiogeographic scale of Udvardy was probably not latitudinal and longitudinal overland migration (dispersion) of elements, which follow the predominantly southward shift of the warm tropical belt. Instead, I visualise a rather more passive vicariant process in association with dispersal in Haffer's (1981) sense, in response to the progressive fragmentation of Pangea. This was followed by continental drift which led to the present configuration of the continents and climates. This suggestion is in accordance with the very poor vagility observed in modern scorpions. II. On the millennial scale, the Pleistocene (post-Pleistocene) biogeography of Udvardy is responsible for the regional level of the biogeographic pattern which, during its settlement, has led to the selection of new lineages and to the extinction of others. III. On the secular scale, the ecological biogeography of Udvardy is a consequence of recent natural or anthropic events. This scale has been little used by scorpion biogeographers, mostly because of lack of data on scorpion life history strategies. In this contribution, examples from scorpions are proposed for and discussed in relation to the three biogeographic scales of Udvardy.

**Key-words:** scorpion – biogeography – phylogeny – palaeobiogeography – Pangea – Laurasia – Gondwanaland – Pleistocene – ecology.

### INTRODUCTION

Attempts to use scorpions as global model organisms in biogeographic studies are not recent. Starting with the classical contributions of, POCOCK (1894), KRAEPELIN (1905) and BIRULA (1917), general biogeographical traits or patterns began to

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established for this taxon of animals, even though the viewpoints of the authors were not totally in accordance.

Regional and local biogeographical contributions then followed (e.g. MELLO-LEITÃO 1945; VACHON 1952; KOCH 1977; FRANCKE 1978; LAMORAL 1979; COUZIN 1981; ARMAS 1982). Most of these failed to demonstrate precise biogeographical patterns or to explain what has been called since POCOCK'S (1894) publication "apparent anomalies in the distribution of some groups of families and genera". The reasons for the inability of these authors to explain better what they observed can probably be attributed to: (i) important gaps in knowledge of the phylogeny of several of the groups studied; (ii) a rejection or an unawareness of Wegener's theory of continental drift propounded in 1912; (iii) apparent ignorance of recent theories concerning climatic vicissitudes, especially in tropical biomes, during the late Cenozoic and Pleistocene periods (these have been used successfully by other tropical biologists over the last 30 years, e.g. MOREAU 1963; PRANCE 1982*b*); (iv) major ignorance of scorpion life history strategies in the sense of MACARTHUR & WILSON (1967) and PIANKA (1970, 1988). Ecologists only started to become aware of scorpion ecology in terms of life history strategies in the late 1970s and early 1980s. This led them to classify many, if not most, scorpions as equilibrium species (POLIS 1990; LOURENÇO 1991). Until the late 1980s (LOURENÇO 1991) these new parameters for scorpion ecology remained the sole preoccupation of ecologists and were ignored by biogeographers.

A more synthetic biogeographical argument is proposed in this paper, based on UDVARDY'S (1981) division of biogeography into three spatio-temporal entities. This is largely because Udvardy's model is clear and didactic (fig. 1). In correlation with Udvardy's model three major biogeographical events may be tentatively used to explain many, or most present patterns observed today among scorpions.

I will not in this contribution try to answer all the difficult questions that have been addressed by biogeographers during the last 100 years. Because of lack of space, only a selected number of examples will be given. My main objective is to suggest to biogeographers (mainly those working with scorpions or Arachnida) the importance of clearly established historical and ecological factors in any biogeographical study.

## 1. PHYLOGENETIC SCALE: PALAEOBIOGEOGRAPHY

The phylogenetic scale encompasses the evolutionary time of all biota and is limited in space only by the size of the earth (UDVARDY 1981). On this scale, only historical factors can be assumed since, for almost all ecological conditions, data are largely or totally unknown. At this level, the evolutionary process of biogeography is, to a considerable extent, a tributary of continental drift and plate tectonics. This new view shook to the foundations the theories of many older paleontologists and biogeographers (UDVARDY 1981).

Both POCOCK (1894) and KRAEPELIN (1905) had made their contributions to scorpion biogeography before the Wegener's theory was propounded in 1912, while BIRULA (1917) probably ignored rather than rejected the theory. Of these authors,

POCOCK at least, in his contribution gives the impression that his intuition would have lead him accept Wegener's theory had he worked a few years later.

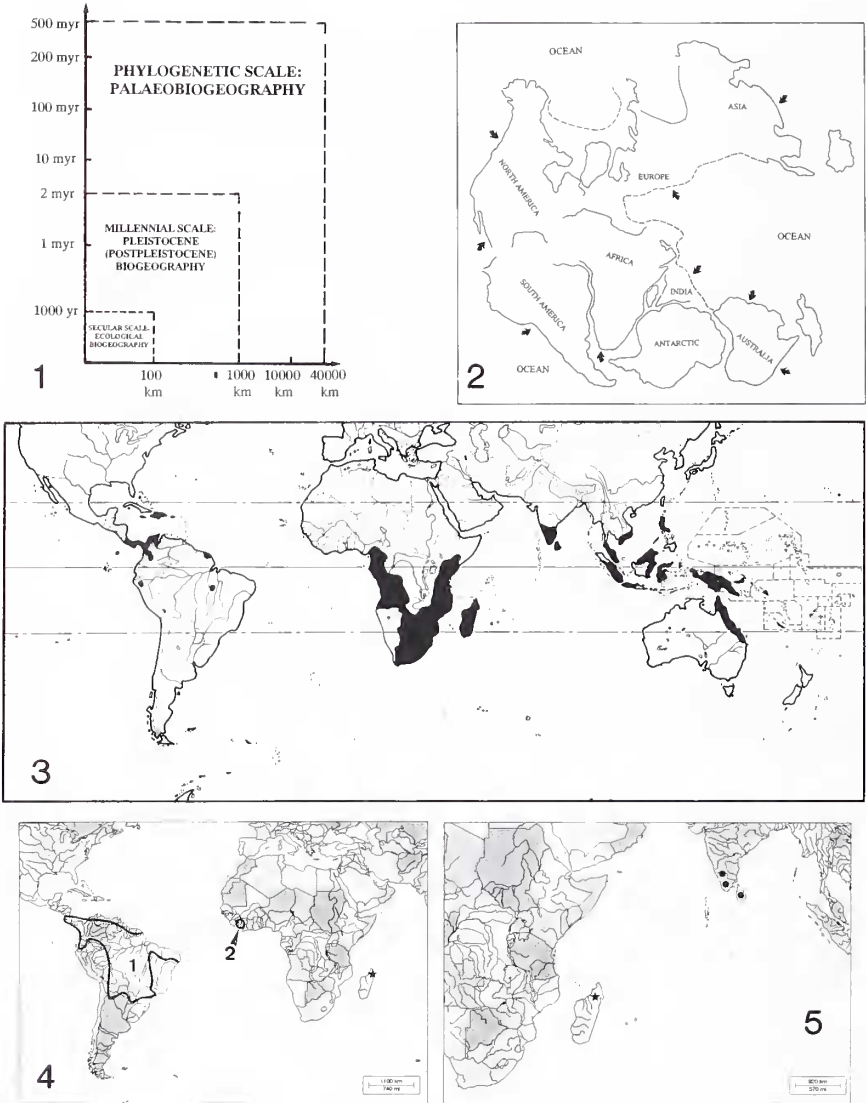
Some subsequent authors, such as MELLO-LEITÃO (1945), also ignored Wegener's theory or were too regional in their approach to take it into consideration. Others, in particular French authors (e.g., FAGE 1929; VACHON 1952; MILLOT 1948), systematically rejected continental drift. In more recent publications authors such as KOCH (1977), LAMORAL (1979, 1980) and COUZIIN (1981) have taken continental drift into consideration when discussing *ad hoc* aspects of regional biogeography<sup>1</sup>.

LAMORAL's (1980) suprageneric classification of recent scorpions, with its discussion of their zoogeography, remains one of the best attempts to explain the general patterns of scorpion biogeography, and was taken in consideration by SISSOM (1990). The zoogeographical suggestions which Lamoral proposes are generally acceptable, i.e., (i) the present global fauna is derived from pulmonate (Neoscorpionina) elements that originated in Laurasia and Gondwanaland during Pangean times (Fig. 2), (ii) the protobuthids were the dominant fauna during Pangean times, and the distribution of present Buthidae is the result of a vicariant process emanating from the fragmentation of Laurasia and Gondwanaland; (iii) the other protoelements, the Chaeriloids and Diplocentroids, also evolved in Laurasia and/or Gondwanaland during Pangean times. The more detailed conclusions of LAMORAL (1980) are, in one way or another, mainly correlated with vicariance and with continental drift. LAMORAL (1980) failed, however, in explaining two points. I. In my opinion he insisted too much on the role of dispersion when affirming that two major factors have influenced speciation and distribution patterns. I agree with the importance of vicariance in response to the progressive fragmentation and continental drift of Pangea and Gondwanaland, but the overland "migration" of Laurasian elements to the north of Gondwanaland needs to be reconsidered. This process of "active" dispersion should be interpreted rather as being a more "passive" process (in Haffer's 1981 dispersal sense)<sup>2</sup>. This opinion is supported by the poor vagility presented by modern species of scorpion<sup>3</sup> (Lourenço 1991). Present biogeographic patterns should be considered more as a the result of different vicariant processes, and as the pieces of an incomplete puzzle. II. Lamoral did not answer the question about "apparent anomalies in the distribution of some groups of families and genera". These "anomalies" have been discussed since the publication of POCOCK's (1894) work. Even today the dis-

<sup>1</sup> A zoogeographical analysis of the world scorpion fauna, based on literature synthesis has been proposed in a recent publication (NENILIN & FET 1992). This contribution (in Russian), which was written in 1983/84 presents, however, several gaps in the bibliography. For this reason, it seems difficult to refer to this paper in the present contribution.

<sup>2</sup> Because of lack of space I will not discuss here the arguments of PLATNICK (1976), UDVARDY (1981) and HAFFER (1981) regarding their personal opinions about the meaning of both dispersion and dispersal (see also LOURENÇO 1986a).

<sup>3</sup> It might be suggested that primitive or aquatic scorpions were better able to disperse than terrestrial forms. They were therefore able to reach many of the shores of Pangea before and during the fragmentation process, since scorpions remained marine (or aquatic) from the Silurian until at least the Triassic (BRIGGS 1987; SHEAR & KULALOVA-PECK 1990).



FIGS 1-5

Fig. 1. Division of biogeography into the three spatio-temporal scales of Udvardy (modified after UDVARDY 1981). Fig. 2. Position of Pangea about 200 my B.P., and hypothetical ways of coastal colonisation by aquatic scorpions. Fig. 3. Gondwanian distribution (in black) of scorpions of the family Ischnuridae (cf. *Opisthacanthus*). Fig. 4. Distribution of the genus *Ananteris* in tropical America (1) and Africa (2), and of the related species of *Tityobuthus* in Madagascar (black star). Fig. 5. Distribution of *Charmus* in India and Sri Lanka (black rounds) and of *Microcharmus* in Madagascar (black star).

junct distributions of Diplocentridae and Iuridae remain unexplained. These families are found in the Neotropics and, respectively, in the Arabian and the Mediterranean regions. The presence of the genus *Opisthacanthus* in both Afrotropical and Neotropical realms was also considered as an "anomaly". The case of the two disjunctly distributed families should be regarded as a result of the previous distribution of protoelements of both families, this result being the consequence of vicariant processes. The exact mechanism of these process has not, however, yet been explained. The patchy distribution of *Opisthacanthus* was finally clarified by LOURENÇO (1985a) who presented all the necessary evidence to suggest that this genus was of typical Gondwanian lineage (Fig. 3), thus invalidating both NEWLANDS' (1973) transatlantic rafting theory and FRANCKE'S (1974) reshuffle, and clearly suggesting that elements of this genus were already present in the African and Brazilian shields of Gondwanaland prior to the continental fragmentation that took place in the second half of the Cretaceous. Further evidence for this pattern of distribution has also been produced for the genus *Ananteris* (LOURENÇO 1985b, 1993). A recent revision on the scorpions of Madagascar (LOURENÇO 1995) brings new evidence of Gondwanian lineages: (i) the demonstration of a close relationship between the Neotropical/ Afrotropical genus *Ananteris* and the genus *Tityobuthus* endemic to Madagascar, and (ii) the discovery of a new genus, *Microcharnus*, closely related to the genus *Charnus* from India and Sri Lanka. These results will be developed in a forthcoming paper on the biogeography of Madagascar (Figs 4 & 5).

In conclusion, I suggest that the main event responsible for determining the biogeographic patterns of scorpions on a palaeogeographic scale, has been the fragmentation of Pangea and subsequent continental drift. The difficulties in explaining the significant discontinuous distribution of the Iuridae and Diplocentridae point not only to the great geological age of most families and genera, but also to the relict faunas and biogeographical patterns which they exhibit today. In the next section I will attempt to explain regional patterns as complements to the palaeobiogeographical scale.

## II. MILLENIAL SCALE: PLEISTOCENE BIOGEOGRAPHY

Since the development of the earth's crust until the Pleistocene epoch several events took place, many of which were related to the continuous drift of the continents. Without citing an exhaustive list, the following can be mentioned: mountain building, differential erosion, epicontinental seas, climatic-vegetational fluctuations, changes of world sea level and the formation of major river systems. All these events took place during the Cenozoic over a period of 60 M.Y., and have influenced the present biogeographical patterns of scorpions. In this section I will make special reference to one of these events, climatic-vegetational fluctuation, which played a major role since the late Cenozoic and which has had a major impact during Pleistocene times<sup>4</sup>. For more details of the consequences of the other events, refer to HAFFER (1981).

<sup>4</sup> For a better understand of the astronomical basis of the climatic oscillations - "Milankovitch cycles" - see HAFFER 1993.

For many years, books and papers about the tropical regions, and in particular about Amazonia, have stated that the biogeographical and diversity patterns observed in these regions could be explained by the long stability of tropical forests over millions of years (FEDEROV 1966; RICHARDS 1969). Subsequent work on geology, paleoclimates and palynology, especially in Amazonia (PRANCE 1982a), has demonstrated that this presumed stability was a fallacy. In fact, although the temperatures in tropical lowlands remained "tropical" during glacial periods (3–5°C lower than today), the forest broke into isolated remnants during cool dry periods (glacial phases). The remnants of forest expanded and coalesced during warm humid periods (interglacial phases). Conversely, nonforest vegetation expanded during glacials and retreated during interglacial phases (as at present). Data from geoscience have been insufficient to indicate the precise areas of changing forests and nonforests and, in particular, the areas in which forests remained during arid phases, presumably serving as refugia for animal and plant populations. Biogeographical studies of neotropical plants and animals indicate several centers of species endemism which are separated by zones of overlap and interbreeding (see PRANCE 1982a). More recent studies on the biogeographical patterns of the Amazonian scorpions (LOURENÇO 1986b, 1987) led to the definition of several endemic centers which are well correlated with the results of PRANCE (1982b) on woody plants, and HAFFER (1969) on birds (Fig. 6).

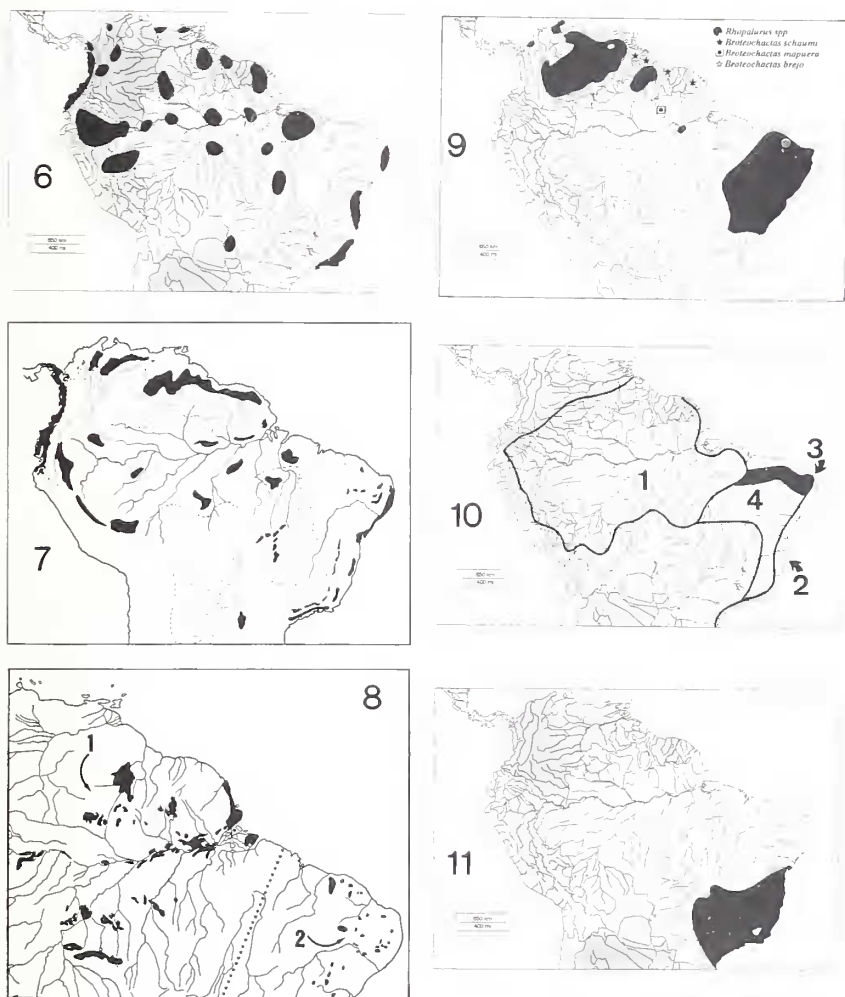
Two biogeographical patterns observed in neotropical scorpions clearly suggest direct correlations with climatic-vegetational fluctuations during the Pleistocene.

#### (i) Polymorphic species in the Amazon region

*Tityus gasci* Lourenço and *Tityus silvestris* Pocock have distributions ranging from French Guyana to Peru and Ecuador. Analysis of the variability of patterns of pigmentation and morphometric values in both species indicates a gradual geographic cline along a transect for *T. gasci*. This species was defined as a clinally polymorphic species, whereas considerable variation which was not well correlated geographically was observed for *T. silvestris* (LOURENÇO 1988; 1994). This type of pattern was first encountered by botanists, and species showing it are termed "ochlospecies"<sup>5</sup> (PRANCE 1982b). According to PRANCE (1982b), ochlospecies are common in many large genera of plants (> 100 species) – *Tityus* has about 120/130 species. Prance suggests that during the dry periods of the paleoclimatic episodes when the forest was reduced to small patches, widespread species became fragmented into several isolated allopatric populations. These isolated populations of ecologically adaptable species (which is the case with some *Tityus* spp.) rapidly recolonized the reestablished forest during wet episodes. Previously isolated populations thereby became contiguous. Temporary reproductive isolation did not produce genetic barriers (at least for woody-plant and scorpions) and only minor morphological differences evolved. Where species reunited the variation was no longer correlated geographically<sup>6</sup>.

<sup>5</sup> From the Greek – *ochlos* = mob + species.

<sup>6</sup> The complex biogeographic patterns observed in several Saharo-Sindian genera of scorpions (VACHON & KINZELBACH 1987), could tentatively be explained in the light of late Cenozoic vicissitudes of the biomes extending from Morocco to India.



FIGS 6-11

Fig. 6. Tropical South America centers of endemism, defined after scorpion distribution patterns. Fig. 7. Hypothetical distribution of forests (black areas) and savannas (white areas) in tropical South America during cool dry periods (modified after AB'SABER 1977). Fig. 8. Distribution of enclaves of savanna inside Amazonia (black areas indicated by 1) and forested islands inside xerophytic formations (black areas indicated by 2). Fig. 9. Examples of disjunct distribution of genera and species in forest and savanna formations. Fig. 10. Relationship between the Atlantic and Amazon forests. 1 and 2 are the present distribution of the Amazon and Atlantic forests. 3 = suggested paleodistribution (strong evidence). 4, suggested paleodistribution (weaker evidence) (modified from BIGARELLA & ANDRADE-LIMA 1982). Fig. 11. Present distribution range of *Tityus serrulatus* in Brazil (black area) over disturbed environments and, suggested original area of distribution (small white area inside black area) prior to recent anthropic influences.

### (ii) Disjunct distributions of scorpion taxa in savanna and rainforest formations

Examples of genera presenting a discontinuous distribution are provided by scorpions which are exclusively adapted to savannas (*Rhopalurus* spp.) or to rainforests (*Broteochoactas* spp.). *Rhopalurus amazonicus* Lourenço is endemic to an enclave of savanna inside the Amazonian rainforest (Fig. 8) whereas *Broteochoactas brejo* Lourenço is found only in a forested island inside arid formations of northeast of Brazil (Fig. 8). These isolated endemic populations provide good evidence for the hypothesis of past connections between the savannas of central Brazil and present enclaves in Amazonia and Guayana (Fig. 9). During past dry periods the savanna formations probably coalesced (Fig. 7). The presence of enclaves of forest (brejos) inside arid formations (Fig. 8) suggests past connections between Amazonia and the Atlantic forest of Brazil (Fig. 10). This hypothesis is supported by the biogeographical pattern in Amazonia presented by scorpions of the genus *Broteochoactas* and by the Chactinae in general (Fig. 9).

### III. SECULAR SCALE: ECOLOGICAL BIOGEOGRAPHY

The analysis of responsible ecological factors in the explanation of the biogeographic patterns of scorpions have been biased for two major reasons: (i) there has been an almost total lack of knowledge of life history strategies until about 15 years ago – knowledge which, until the late 1980s, was almost the only preoccupation of ecologists, and (ii) a generalized opinion, even among modern biologists, according to which scorpions are ecologically plastic organisms capable of withstanding radical changes in environmental conditions, and therefore of being very good colonisers. This second assumption is a fallacy. With our growing knowledge of scorpion life history strategies it can be seen that many if not most scorpions are undoubtedly equilibrium species which tend to inhabit stable and predictable natural environments, produce single egg clutches, do not store sperm, have long life-spans, present low population densities, have a very low  $r_{max}$ , show weak mobility, and are highly endemic, often known from a single locality.

In contrast some scorpions are opportunistic species, such as certain members of the genera *Centruroides*, *Tityus* and *Isometrus*. These exhibit marked ecological plasticity and are readily capable of invading disturbed environments. They produce multiple clutches from a single insemination, have elaborate sperm storage capabilities (KOOVOR *et al.* 1987), short embryonic development, short life spans, high population densities, rapid mobility, and are widely distributed. These opportunistic species are of little use for establishing biogeographical patterns, although fortunately they can readily be identified and disregarded.

Opportunistic species evolve mainly in disturbed and unpredictable environments which are the result of natural (e.g. volcanic activity) or anthropic action. Long known examples include the presence of a population of the neotropical species *Centruroides gracilis* (Latreille) in the Canary Islands (KRAEPELIN 1905; LOURENÇO 1991) and the worldwide distribution of the Indo-Malayan scorpion *Isometrus*



*maculatus* (DeGeer) which has been transported by human agency during the last four centuries and is today present in almost all tropical coastal regions. Some elements have even been found at a distance of 3000 km upstream of the delta of the River Amazon (LOURENÇO 1991). The phenomenon of the replacement of species is well illustrated in several islands of the Caribbean, where natural volcanic activity and human impact are important. In this region, many endemic populations of equilibrium species are regressing or have disappeared, to be replaced by opportunistic species of the genus *Ceutruroides* which now occupy most of the Islands (LOURENÇO 1992).

In continental regions, opportunistic species can rapidly occupy habitats disturbed by human activities, where the original native species have been selected against, thus leaving their ecological niches vacant. This kind of situation can be observed in Brazil and Mexico where very dense populations of species as *Tityus serrulatus* Lutz & Mello and *Ceutruroides suffusus* Pocock, respectively, occupy large geographic areas. When this phenomenon of secondary succession is associated with noxious, opportunistic species, public health problems can arise (LOURENÇO & CUELLAR 1995; LOURENÇO & CLOUDSLEY-THOMPSON 1996).

## CONCLUSIONS

Although the presence of a reduced number of opportunistic scorpion species may not be a good indication of predictable biogeographic patterns, many or most scorpions are equilibrium species and can be useful models in biogeographical research. Several factors make scorpions useful for biogeographical (or biodiversity) studies, as suggested by Noss (1990): (i) stable taxonomy, at least for some regions of the world; (ii) life history strategies that are well understood; (iii) the fact that individuals can readily be observed in the field with the use of UV light, and (iv) biogeographical and endemic patterns that are well correlated with those of other taxa of animals and plants (see LOURENÇO 1987). Scorpion biogeographers, however, need to be more aware, in their interpretations, of the distinction between the historical and the ecological factors responsible for the biogeographical patterns observed.

In conclusion, the definition of biogeographical (or biodiversity) patterns is a matter for specialists. The number of experienced specialists is drastically decreasing in many countries mostly because of lack of interest from governmental and academic authorities. The time required for the adequate training of students in evolutionary biogeography is long – up to 10 or 15 years. In consequence, this situation threatens to generate important gaps in this discipline (LOURENÇO & BLANC 1994).

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## REFERENCES

- AB'SABER, A.N. 1977. Espaços ocupados pela expansão dos climas secos na America do Sul, por ocasião dos períodos glaciais quaternários. *Paleoclimas* 3, IGEOG-USP: 1-19.
- ARMAS, L.F. 1982. Algunos aspectos zoogeograficos de la escorpiofauna antillana. *Poeyana* 238: 1-17.
- BIGARELLA, J.J. & D. ANDRADE-LIMA 1982. Paleoenvironmental changes in Brazil. In: G.T. PRANCE (ed.), *Biological Diversification in the Tropics*, pp. 27-40. *Columbia University Press, New York*.
- BIRULA, A. 1917. Fauna of Russia and adjacent countries. Arachnoidea I. 1. Scorpions. Fauna Rossii, St. Petersburg. *Académie des Sciences, Musée de Zoologie*: 1-154. (Translated by IPST, Jerusalem 1965, IPST Cat. N° 1207).
- BRIGGS, D.E.G. 1987. Scorpions take to the water. *Nature* 326: 645-646.
- COUZIIN, H.W.C. 1981. Revision of the genus *Heterometrus* Hemprich & Ehrenberg (Scorpionidae, Arachnidea). *Zoologische Verhandlungen Leiden*, 184: 1-196.
- FAGE, L. 1929. Les Scorpions de Madagascar. *Faune des Colonies françaises* 3: 637-694.
- FEDEROV, A.A. 1966. The structure of the tropical rain forest and speciation in the humid tropics. *Journal of Ecology* 54: 1-11.
- FRANCKE, O.F. 1974. Nota sobre los géneros *Opisthacanthus* Peters y *Nepabellus* nom. nov. (Scorpionida, Scorpionidae) e informe sobre el hallazgo de *O. lepturus* en la Isla del Coco, Costa Rica. *Brenesia* 4: 31-35.
- FRANCKE, O.F. 1978. Systematic revision of diplocentrid scorpions (Diplocentridae) from Circum-Caribbean lands. *Special Publications. Museum, Texas Tech University* 14: 1-92.
- HAFFER, J. 1969. Speciation in Amazonian forest birds. *Science* 165: 131-137.
- HAFFER, J. 1981. Aspects of Neotropical bird speciation during the Cenozoic. In: *Vicariance biogeography: a critique*. G. NELSON & D.E. ROSEN (Eds.). *Columbia University Press*, pp. 371-412.
- HAFFER, J. 1993. Time's cycle and time's arrow in the history of Amazonia. *Biogeographica* 69(1): 15-45.
- KOCH, L.E. 1977. The taxonomy, geographic distribution and evolutionary radiation of Australian-Papuan scorpions. *Records of the Western Australian Museum* 5(2): 83-367.
- KOVOOR, J., W.R. LOURENÇO & A. MUÑOZ-CUEVAS 1987. Conservation des spermatozoïdes dans les voies génitales des femelles et biologie de la reproduction des Scorpions (Chélicérates). *Compte-rendu hebdomadaire des séances de l'Académie des sciences, Paris*: 304, sér. III, 10, 259-264.
- KRAEPELIN, K. 1905. Die geographische Verbreitung der Scorpione. *Zoologische Jahrbücher, Systematik, Ökologie und Geographie des Tiere* 22: 321-364.
- LAMORAL, B.H. 1979. The scorpions of Namibia (Arachnida: Scorpionida). *Annals of the Natal Museum* 23(3): 497-784.
- LAMORAL, B.H. 1980. A reappraisal of suprageneric classification of recent scorpions and of their zoogeography. *Verhandlungen des 8. Internationalen Arachnologen-Kongresses*, Wien, 1980: 439-444.
- LOURENÇO, W.R. 1985a. Essai d'interprétation de la distribution du genre *Opisthacanthus* (Arachnida, Scorpiones, Ischnuridae) dans les régions néotropical et afrotropical. Étude taxinomique, biogéographique, évolutive et écologique. *Thèse de Doctorat d'Etat, Université Pierre et Marie Curie*: 287 pp.
- LOURENÇO, W.R. 1985b. Le véritable statut des genres *Ananteris* Thorell, 1891 et *Ananteroides* Borelli, 1911 (Scorpiones, Buthidae). *Annales of the Natal Museum* 26(2): 407-416.
- LOURENÇO, W.R. 1986a. La vicariance biogéographique chez les Scorpions néotropicaux. *Bulletin d'Ecologie* 17(3): 161-172.

- LOURENÇO, W.R. 1986b. Diversité de la faune scorpionique de la région amazonienne; centres d'endémisme; nouvel appui à la théorie des refuges forestiers du Pléistocène. *Amazoniana* 9(4): 559–580.
- LOURENÇO, W.R. 1987. Les modèles évolutifs des Scorpions néotropicaux et la théorie des refuges forestiers du Pléistocène. *Compte-rendu des séances. Société de biogéographie* 63(3): 75–88.
- LOURENÇO, W.R. 1988. Diversité biologique et modalités de la spéciation chez les Scorpions amazoniens; *Tityus silvestris* Pocock, un cas particulier de polymorphisme. *Compte-rendu hebdomadaire des séances de l'Académie des sciences, Paris*, 306, sér., 3: 463–466.
- LOURENÇO, W.R. 1991. Biogéographie évolutive, écologie et les stratégies biodémographiques chez les Scorpions néotropicaux. *Compte-rendu des séances. Société de biogéographie* 67(4): 171–190.
- LOURENÇO, W.R. 1992. Les peuplements des Scorpions des Antilles; facteurs historiques et écologiques en association avec les stratégies biodémographiques. *Studies on Neotropical Fauna and Environment* 27(1): 43–62.
- LOURENÇO, W.R. 1993. A review of the geographical distribution of the genus *Ananteris* Thorell (Scorpiones, Buthidae), with description of a new species. *Revista de biologia tropical* 41(3): 697–701.
- LOURENÇO, W.R. 1994. Biogeographic patterns of tropical South American scorpions. *Studies on Neotropical Fauna and Environment* 29(4): 219–231.
- LOURENÇO, W.R. 1995. Description de trois nouveaux genres et de quatre nouvelles espèces de Scorpions Buthidae de l'île de Madagascar. *Bulletin du Muséum National d'Histoire Naturelle, Paris*, 4e sér., 17(1-2): 95-106.
- LOURENÇO, W.R. & C.P. BLANC 1994. Biodiversité et biogéographie évolutive. *Biogeographica* 70(2): 49–57.
- LOURENÇO, W.R. & J.L. CLOUDSLEY-THOMPSON 1996. Effects of human activities on the environment and their influence on the distribution of dangerous species of scorpions. *Proc. 1st. International Congress on Envenomations. Inst. Pasteur, Paris*.
- LOURENÇO, W.R. & O. CUELLAR 1995. Scorpionism, life history strategies and parthenogenesis. *The Journal of Venomous Animals and Toxins* 1(2): 51-62.
- MACARTHUR, R.H. & E.O. WILSON 1967. The theory of island biogeography. *Princeton University Press, Princeton, New Jersey*, 203pp.
- MELLO-LEITÃO, C. 1945. Escorpiões sul-americanos. *Arquivos do Museu nacional Rio de Janeiro*, 40: 1–468.
- MILLOT, J. 1948. Revue générale des Arachnides de Madagascar. *Mémoires de l'Institut scientifique de Madagascar*, Sér. A 1(2): In: *Mémoires de la Société de biogéographie* (1953): 127–145.
- MOREAU, R.E. 1963. Vicissitudes of the African biomes in the late Pleistocene. *Proceedings of the Zoological Society London* 141: 395–421.
- NENILIN, A.B. & V.Y. FET 1992. Zoogeographical analysis of the world scorpion fauna (Arachnida, Scorpiones). *Arthropoda Selecta* 1(2): 3–31.
- NEWLANDS, G. 1973. Zoogeographical factors involved in the trans-atlantic dispersal pattern of the genus *Opisthacanthus* Peters (Arachnida: Scorpionida). *Annals of the Transvaal Museum* 28(7): 91–98.
- NOSS, R.F. 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology* 4: 355–364.
- PIANKA, E.R. 1970. On r- and K-selection. *American Naturalist* 104: 592–597.
- PIANKA, E.R. 1988. Evolutionary Ecology. *Harper & Row Publ. New York*, pp. 1–468.
- PLATNICK, N. 1976. Concepts of dispersal in historical biogeography. *Systematic Zoology* 25(3): 294–295.

- POCOCK, R.I. 1894. Scorpions an their geographical distribution. *Natural Science* 4(27): 353–364.
- POLIS, G.A. 1990. Ecology. *In: The Biology of Scorpions*. G.A. POLIS (ed.) *Stauford Uuiversity Press, Stauford*, pp. 247–293.
- PRANCE, G.T. 1982a (Ed.). Biological diversification in the tropics. *Columbia University Press, New York*, 714 pp.
- PRANCE, G.T. 1982b. Forest refuges: Evidence from woody angiosperms. *In: G.T. PRANCE (ed.), Biological diversification in the tropics. Columbia University Press, New York*, pp. 137–158.
- RICHARDS P.W. 1969. Speciation in the tropical rain forest and the concept of the niche. *Biological Journal of the Linnean Society of Loudon* 1: 149–153.
- SHEAR, W.A. & J. KOKALOVA-PECK 1990. The ecology of Paleozoic terrestrial arthropods: the fossil evidence. *Canadian Journal of Zoology* 68:1807–1834.
- SISSOM, W.D. 1990. Systematics, Biogeography, and Paleontology. *In: the Biology of Scorpions*. POLIS, G.A. (ed.), *Stauford University Press, Stauford*, pp. 64–160.
- UDVARDY, M.D.F. 1981. The riddle of dispersal: dispersal theories and how they affect vicariance biogeography. *In: Vicariance biogeography: a critique*. G. NELSON & D.E. ROSEN (Eds.), *Columbia University Press*, pp. 6–39.
- VACHON, M. 1952. Etudes sur les Scorpions. *Institut Pasteur Algérie, Alger*: 482 pp.
- VACHON, M. & R. KINZELBACH 1987. On the taxonomy and distribution of the scorpions of the Middle East. *Proceedings of the Symposium on the Fauna and Zoogeography of the Middle East*. F. KRUPP, W. SCHNEIDER & R. KINZELBACH (Eds.). *L. Reichert Verlag, Wiesbaden*, pp. 91–103.